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Seasonal dynamics of autotrophic respiration in boreal forest soil estimated by continuous chamber measurements

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Soils contain a large C pool, but temporal changes in the pool size are difficult to determine. Root and rhizosphere respiration (R_a) is a major component of soil C-balance, but it cannot be measured continuously with conventional methods. Here, we present a novel method for determining the contribution of R_a. This novel method is based on temperature fitting of soil CO_2 effluxes (F_0) over long and short time intervals using continuous chamber measurements. We show the contribution of seasonal changes to R_a and to total soil CO_2 efflux in a Scots pine forest in southern Finland. R_a contributed about 42% of the total soil CO_2 efflux. The seasonally extremely variable contribution from 17% in early April to 60% in late July followed the seasonal pattern of the GPP. The contribution of R_a was 45% of the annual total GPP (1154 g C m^{-2}) of the forest ecosystem. The increase in R_a lagged behind the increase in GPP by 18 days, and the peak in R_a was observed about six weeks after the highest values of daily GPP were attained, which reflected the changes in the seasonal pattern in above- and below ground-allocation of assimilated C.

Introduction

Worldwide, soils contain 1500–2400 Pg of carbon (C) (Batjes *et al*. 1996) which is a substantial amount as compared with 828 Pg of carbon in atmospheric carbon dioxide (CO_2) (Prather *et al*. 2012, Joos *et al*. 2013). Thus, changes in the soil C stock have an effect on the atmospheric CO_2 (Kirschbaum 2000, Luyssaert *et al*. 2007). However, the changes taking place in the soil C stocks are extremely difficult to measure, because in large stocks and within a short time interval they are rather small. In addition, the spatial variation in the soil C content and bulk density is large, which makes it difficult to determine changes in C stocks on an annual or even on a decadal scale.

There are two major approaches for detecting changes in soil C stocks. The first approach is based on observing the actual changes in the amounts of soil C based on repeated inventory measured over certain time intervals. In order to be successful, this method sets high requirements for sampling design and usually a very large number of soil samples are required to determine small changes in soil C stocks. The second approach is to measure CO_2 fluxes between the soil and atmosphere. This approach has been widely used in C balance studies in various ecosystems (Elsgaard *et al*. 2012, Ilvesniemi *et al*.

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2009, Luyssaert *et al*. 2007, Ojanen *et al*. 2012, Zha *et al*. 2007). The soil CO_2 efflux consists of two major components, respiration that originates from the decomposition of soil organic matter and respiration that originates from roots and associated mycorrhizal fungi. Reliable separation of these two components is needed to be able to estimate changes in soil C stocks based on soil CO_2 efflux.

The most common method of partitioning soil respiration into its components is trenching which entails the roots being cut (Epron *et al*. 1999ab, Kuzyakov 2006). Another method is to prevent the flow of carbohydrates to the root system by isolating the phloem connection of the tree stems by girdling (Högberg *et al*. 2001). Both of these methods are destructive and cannot be repeated in the same measurement plot after the root system has been affected (Minkkinen *et al*. 2007). They may also result in changes in the microbial community composition that progress from ectomycorrhizal to saprophytic fungi (Siira-Pietikäinen *et al*. 2003), which make the comparison with undisturbed soil-root systems to interpret difficult. Similar problems eventually arise with girdling, when the trees at the girdled site start to die. These methods are not suitable for long-term or continuous monitoring because the conditions in control and trenched (or girdled) plots change after the initial trenching. The regrowth of roots from neighbouring trees after girdling takes place in due course. Both methods may also change the soil water conditions because the transpiration flows of the treated trees are stopped.

The contribution of root and rhizosphere respiration has also been investigated by using the stable isotope ^{13}C or radioactive isotope ^{14}C, which can be traced from the respiration (Bowling *et al*. 2002, Schuur and Trumbore 2006, Kodama *et al*. 2008). Knowing the $\delta^{13}C$ signature of measured CO_2 efflux, along with its component fluxes and flux rate enables the estimation of the proportions of root and rhizosphere respiration and respiration that originates from the decomposition using a mixed model approach. However, this requires that the $\delta^{13}C$ signature of the component fluxes (root and rhizosphere respiration and respiration originating from the decomposition) are accurately known. Alternatively the contribution of root and rhizosphere respiration to total respiration can also be studied by adding a known amount of ^{13}C or ^{14}C isotope into the assimilated CO_2 and then tracing it back from the respiration (Epron *et al*. 2012).

Several tracer experiments using stable or radioactive C were conducted during the last years for determining the contribution of root and rhizosphere respiration, based either on pulse labeling or continuous labeling (Bahn *et al*. 2009, Pumpanen *et al*. 2009, Ruehr *et al*. 2009, Subke *et al*. 2009, Heinonsalo *et al*. 2010, Epron *et al*. 2012). These labeling studies were targeted at partitioning the carbon fluxes between above- and below-ground parts of plants. This approach enables disentangling the respiration that originates from the decomposition of soil organic matter (SOM) and respiration originating from the respiration of root tissue and recent assimilates and root exudation. However, pulse labeling experiments are rather laborious, and they cannot be conducted repeatedly in the same locations. Thus, another but less destructive method that enables the continuous monitoring of root and rhizosphere respiration would be necessary for long term monitoring of the seasonal changes in the autotrophic and heterotrophic components of soil respiration.

Soil CO_2 efflux is usually modeled by using nonlinear regression models that take into account soil temperature only (Hamdi *et al*. 2013, Lloyd and Taylor 1994, Tuomi *et al*. 2008) or treat soil temperature and soil moisture as confounded factors (Davidson *et al*. 1998, Pumpanen *et al*. 2003b). However, the substrate availability has a confounding effect on the response of soil respiration to temperature when it varies with measurement temperature (Kirschbaum 2006). This is particularly important in boreal forests where biological activity has a strong seasonal cycle. During the winter the vegetation is dormant, and most of the respired CO_2 originates from the decomposition of detritus, whereas in the summer the vegetation is active and introduces easily decomposable C into the soil. Reichstein *et al*. (2005) demonstrated that the long-term and short-term temperature responses in ecosystem respiration are very different from each other in ecosystems such as boreal forests that have distinct seasonal patterns in photosynthesis and res-

piration. Those authors developed an algorithm whereby 15-d time periods were used to estimate the temperature sensitivity of respiration in different forest ecosystems across Europe and compared these with the annual temperature response. In the case of summer-active ecosystems such as summer-green deciduous forest or a summer-crop ecosystem, the seasonal co-variation of temperature with general biological activity resulted in an overestimation of the direct short-term temperature sensitivity of respiration (Reichstein *et al*. 2005). Root and rhizosphere respiration is to a large extent driven by recent photosynthates (Högberg *et al*. 2001) and photosynthesis has a distinct seasonal variation, thus the differences in the temperature response of short term and long term respiration (soil CO_2 efflux) can be used as a surrogate for estimating the contribution of soil CO_2 efflux that originates from recent photosynthesis (Pumpanen *et al*. 2008). The method is based on the assumption that the seasonal apparent temperature response does not reflect the actual short-term (hour-to-hour) temperature response. This is assumed because the response is confounded by other factors that co-vary with temperature such as phenology of vegetation and subsequent seasonal cycle in the assimilation of carbon (Reichstein *et al*. 2005). The apparent seasonal temperature response is higher than the short-term temperature response, because the high soil CO_2 effluxes in the summer are due to high temperatures and also higher C allocation to fine roots and mycorrhizal fungi (Boone *et al*. 1998, Högberg *et al*. 2001). The low interference with the measured system allows this method to be used on a continuous basis over long time intervals. The method also enables the investigation of the seasonal variation in the proportion of root and rhizosphere respiration. Measuring this ratio is an important determinant especially in boreal forests, which are typical summer-active ecosystems.

In this study, we investigated the applicability of this method for separating the autotrophic and heterotrophic components in soil respiration on a continuous basis over a long period. We also determined the seasonal time lags between the onset of photosynthesis in the spring and soil respiration and in particular between the autotrophic respiration and gross primary productivity (GPP). We hypothesized that the start of autotrophic respiration is delayed related to the heterotrophic respiration in the spring because the trees allocate more photosynthates to the construction of new needles and shoots in the spring (Lippu *et al*. 1994, Konôpka *et al*. 2005).

Material and methods

Measurement site

All measurements were performed at SMEAR II (Station for Measuring Forest Ecosystem–Atmosphere Relations II) in a 51-year-old boreal coniferous forest stand in southern Finland (61°51´N, 24°17´E, 180 m a.s.l.). Material and energy fluxes within the forest stand and between the forest and the atmosphere have been monitored intensively at the site since 1996 (Hari and Kulmala 2005). The annual mean temperature of the area is +3.5 °C; February is the coldest month (mean –7.7 °C) and July is the warmest (mean +16.0 °C). The annual precipitation mean is 711 mm and the two wettest months are July (92 mm) and August (85 mm) (Pirinen *et al*. 2012). The site was sown with Scots pine (*Pinus sylvestris*) seeds in 1962 on burned, mechanically prepared soil. The basal area of the stand is 23 m^2 ha^{-1} and the dominant trees have a mean diameter at breast height of 19.6 cm. The canopy height is about 17.5 m (Bäck *et al*. 2012). The soil is a Haplic podzol on glacial till (FAO 1990), which overlies homogeneous bedrock of at mean depth of 0.6 m which prevents the vertical movement of water and air. The C content of the organic soil layer in the top of the mineral soil is 300 mg g^{-1} and in the A-horizon it is 60 mg g^{-1} which decreases to 3 mg g^{-1} in the lower part of the B-horizon. The biomass inventory (Ilvesniemi and Liu 2001) indicated the total surface area of the roots < 2 mm to be generally about 3.5 m^2 m^{-2} in the organic soil layer, 1.8 m^2 m^{-2} in the A-horizon and about 0.8 m^2 m^{-2} in the B-horizon. The dominant species in the field-layer vegetation are *Vaccinium myrtillus* and *Vaccinium vitis-idaea*. The ground vegetation consists mainly of mosses *Dicranum polysetum*, *Hylocomium splendens* and *Pleurozium schreberi*, which overlie a 0.05 m layer of soil humus.

Fig. 1. Automated measurement chamber used in this study. The chamber sits in an aluminium frame, which is pushed into the litter layer and anchored to the soil.

Chamber measurements

We used three automated closed chambers for continuous soil CO_2 efflux measurements. The chamber consists of a transparent box (20 cm × 20 cm × 25 cm) made of 6-mm-thick acrylic that was positioned on an aluminum frame (7 cm in hight), which was inserted into the litter layer of the soil (Fig. 1). The chamber was tested against ambient CO_2 effluxes according to the protocol described in Pumpanen *et al*. (2004). Two of the chambers were transparent, and one was covered with aluminum foil to prevent the light from entering the chamber. Thus, the daytime values in the transparent chambers represent the net CO_2 exchange of the forest floor. These resulted from the difference between the CO_2 uptake and respiration of ground vegetation and soil CO_2 effluxes, and the nighttime soil CO_2 efflux values and respiration of ground vegetation. Plants were not removed from the chamber.

Between the measurements, the air inside the chamber was mixed continuously by a small fan (2.5 cm in diameter). The CO_2 concentration inside the chamber was recorded with a GMP343 diffusion type CO_2 probe (Vaisala Oyj, Vantaa, Finland) which has a measurement range of 0 to 1000 ppm. The GMP343 CO_2 probes are based on Vaisala's CARBOCAP sensor technology (Vaisala Oyj., Vantaa, Finland). The sensor used was a non-dispersive infrared (NDIR) sensor for the measurement of gaseous CO_2. The relative humidity inside the chamber was recorded continuously with semiconductor sensor (HIH-4000, Honeywell International, Inc.) and temperature with a thermocouple type K sensor.

Between the measurements, the chamber was tilted to the side of the frame by an electric motor (E192.24.625, Micro Motors, Mid Glamorgan, UK) so that the soil and the vegetation under the chamber remained intact. For the measurements, the box was turned gently on the frame by the electric motor. All the chambers were closed for 3.5 minutes every 30 minutes. The data from the automated chambers were recorded at 5-second intervals by AD converters (Nokeval, Nokeval Oy, Nokia, Finland) and stored in a computer memory.

The spatial representativeness of the automated chambers was also verified by manual chamber measurements that were taken at two-week intervals on 14 permanent measurement plots located in the same area. The manual chamber used in the study (20 cm diameter and 30 cm height) was equipped with a small fan and covered with aluminum foil to exclude sunlight. The CO_2 concentration in the chamber headspace was measured using GMP343 CO_2 probes (Vaisala Oyj, Vantaa, Finland). The CO_2 concentration readings were recorded at 5-second intervals and corrected automatically for humidity, temperature and pressure with a data recorder (MI70, Vaisala Oyj, Vantaa, Finland). The humidity and temperature values used for the correction were obtained from a temperature and humidity probe (HMP75,Vaisala Oyj, Vantaa, Finland) that had

been attached to the inside of the chamber and connected to the MI70 data recorder (Kulmala *et al*. 2008). During the measurements, the chamber was attached for 5 minutes to a collar made of high density polyethene (20.5 cm diameter and 5 cm height). The CO_2 efflux was calculated by linear fitting against time and CO_2 concentration inside the chamber headspace.

Eddy covariance flux measurements and calculation of GPP

We derived the gross primary productivity (GPP) from continuous net ecosystem exchange (NEE) measurements using the eddy covariance (EC) method. In the EC system, the anemometer and the sample tube intake were installed above the stand at a height of 23 m. The instrumentation was documented in more detail in Vesala *et al*. (2005) and the post processing of the data in Mammarella *et al*. (2009). We derived the GPP from half-hourly NEE measurements according to the same protocol as described in detail in Kolari *et al*. (2009). In short, the half-hourly mean NEE was filtered using turbulence criteria described in Markkanen *et al*. (2001) and corrected for changes in storage of CO_2 below the measuring height. We partitioned NEE into ecosystem respiration (R_e) and gross primary productivity (GPP) R_e by using a modified Arrhenius type exponential equation (Lloyd and Taylor 1994):

$$R_e = r_0 e^{E\left(1-\frac{T_0}{T_s}\right)}, \quad (1)$$

where T_s is temperature at a depth of 3 cm in the soil organic layer, r_0 the mean nighttime turbulent flux at soil temperature T_0, and E is the temperature sensitivity parameter. We used half-hourly fluxes that fulfilled the turbulence criteria for deriving GPP directly from the measured NEE thus:

$$\mathrm{GPP} = -\mathrm{NEE} + R_e. \quad (2)$$

During periods of weak atmospheric mixing, we estimated the GPP by using an empirical big-leaf model that had been parameterized for the GPP obtained directly from the measured fluxes. The GPP was modeled as a function of light with a nonrectangular hyperbola:

$$\mathrm{GPP} = \frac{1}{2\theta}\left[\alpha I + P_{\max} - \sqrt{(\alpha I + P_{\max})^2 - 4\theta\alpha I P_{\max}}\right], \quad (3)$$

where I is the incident photosynthetically active radiation (PAR), P_{max} is the rate of saturated photosynthesis, θ is the parameter defining the convexity of the light response curve, and α is the initial slope of the curve. The temperature sensitivity of respiration was derived from the regressions of accepted nighttime turbulent fluxes against temperature in the soil organic layer. The P_{max} to α ratio, i.e. the curvature of the photosynthetic light response, was smoothed over the whole year as running means of 60 days, and daily values of r_0, α and P_{max} were re-estimated using the fixed seasonal course of P_{max}/α.

Soil temperature and moisture

We recorded soil temperatures at 15-min intervals using silicon temperature sensors (Philips KTY81-110, Philips semiconductors, Eindhoven, the Netherlands) that had been installed in the middle of the organic layer and eluvial horizons at depths of 3 cm and 7 cm. The temperatures were measured over 1 h periods. Volumetric water content was monitored in respective soil layers at hourly intervals using the TDR-method with unbalanced steel probes connected to cable radar (TDR-100, Campbell Scientific Ltd., Logan, Utah).

The respiration components

The CO_2 exchange rates inside the chamber were calculated from linear fitting of time *vs*. temperature-, pressure- and humidity-corrected CO_2 concentration during 3-minutes closure times. Soil temperature and water content were the means of seven probes installed in each soil horizon at the measurement site. We studied the apparent temperature responses of respiration in three soil CO_2 efflux chambers on different temporal scales with an exponential function of the form:

$$R = r_b Q_{10}^{T/10}, \quad (4)$$

where R is the soil respiration, T is the temperature and r_b and Q_{10} are the fitted parameters. We studied the effects of recent photosynthate on soil respiration, by basing our calculations on the technique presented by Reichstein *et al*. (2005) and Pumpanen *et al*. (2008). We fitted the short-term temperature responses in 7-day periods over a 7-month-long period when the automated chambers were in operation (from the beginning of May until late November). We assumed that the temperature responses fitted over the 7-day windows mainly represent the production of CO_2 from detrital matter, whereas the seasonal cycle of the soil CO_2 efflux reflected concomitant changes in both autotrophic and heterotrophic respiration components. The long-term temperature response fitted over the whole measuring period from May to November was used for calculating the total CO_2 efflux F_0 from the soil.

The amounts of recent photosynthate slowly increased in the course of spring along with the increasing photosynthesis and decreased in the autumn with decreasing photosynthesis. This pattern of changes can also be seen in root and rhizosphere respiration on a longer time scale (Boone *et al*. 1998, Högberg *et al*. 2001). The observed transfer times of recent photosynthates from the tree shoots to roots has been shown to be between two days and one week (Horwath *et al*. 1994, Mikan *et al*. 2000, Ekblad *et al*. 2005, Knohl *et al*. 2005, Vargas *et al*. 2010). The changes in photosynthetic production may transfer even faster to root and rhizosphere respiration through the propagation of pressure waves in the phloem (Mencuccini and Hölttä 2010). We assumed that the contribution of a recent photosynthate during a 7-day period remains stable and the CO_2 emission during this period reflects the variation in temperature and not the increase of labile substrates such as root exudates.

We took the Q_{10} values obtained with the long and short term fitting, and estimated the contribution of recent photosynthate (r_a) to total soil respiration following the method described by Pumpanen *et al*. (2008). The contribution of R_a at moment t was obtained by the following equation:

$$R_a(t) = F_0(t) - r_0 Q_{10h}^{T(t)/10}, \quad (5)$$

where F_0 is the total soil CO_2 efflux measured in automated chambers at the moment t, and the term on the right hand side is the heterotrophic respiration (thereafter marked with R_h). It is calculated using r_0 that is the basic level of respiration in the soil which originates from the decomposition of soil organic matter and maintenance respiration by the roots. r_0 was obtained from the 7-day temperature response fittings in the last two weeks of May when the soil temperatures were still low, and the below-ground allocation of recent photosynthates was still low as compared with the above-ground C allocation (Konôpka *et al*. 2005, Lippu *et al*. 1994). Q_{10h} is the mean of Q_{10} values determined over the 7-day periods, and $T(t)$ is the mean temperature of soil O- and A-horizons (where most of the roots are concentrated) at the moment t.

We used the calculation described above for all the dark-chamber data. We also used the dark chamber to cover the whole diurnal variation in soil CO_2 efflux. Then, we also calculated the temperature responses of nighttime soil CO_2 efflux data of the two transparent chambers by using the values measured after sunset and before sunrise in a similar manner. Only nighttime data were used for the transparent chambers, where the daytime CO_2 effluxes represented net ecosystem exchange of the forest floor including the soil and plant respiration, along with the photosynthesis of the ground vegetation. The temperature responses of all three automated chambers are presented in Fig. 2.

The R_a calculated from the nighttime data of the two transparent chambers was used to estimate the standard error of the R_a estimates for the three chambers. Similarly, we calculated the standard error for the flux measurements in the manual chambers. We used Pearson's correlation to study the dependence between the manual and automated chambers. The correlation analysis was carried out by using the mean CO_2 effluxes of the 14 manual chambers and the CO_2 effluxes from the darkened automated chamber for the respective time moments. Finally, the differences, between the short term Q_{10h} values in the three automated chambers were tested with one-way ANOVA followed by Tukey's HSD *post hoc* test. Equality of variances was verified with Levene's test. Statistical tests and the fitting of tem-

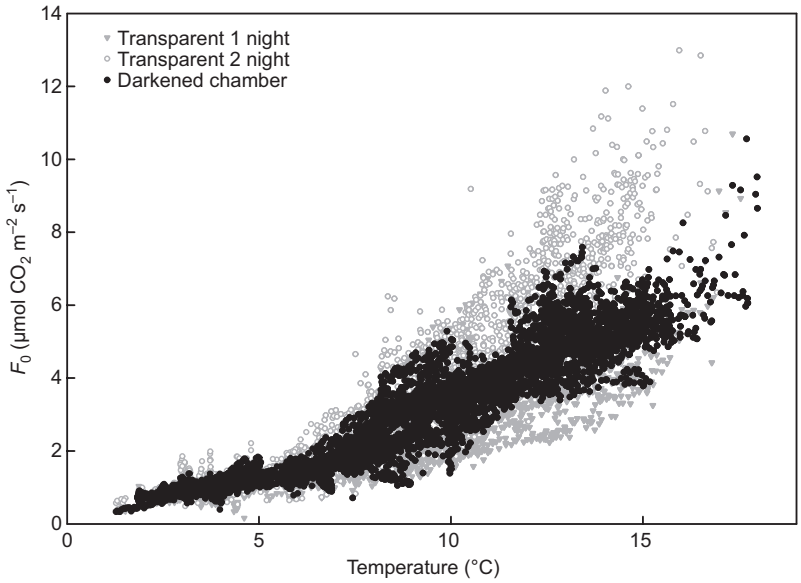

Fig. 2. Temperature response of hourly soil CO_2 effluxes in the automated chambers in 2012. The dark chamber was covered by aluminum foil whereas the other two chambers were kept transparent. The figure is only for the nighttime effluxes of the transparent chambers.

perature responses of soil respiration (Eqs. 4–5) were performed using the PASW 18.0 statistical software (SPSS Inc., Chicago, IL). The partitioning of NEE to R_e and GPP was accomplished with Matlab R2012a (MathWorks, Natick, MA).

Results

Seasonal variation in soil CO_2 efflux

Soil CO_2 effluxes had a seasonal pattern; the daily means varied from ~1 μmol m^{-2} s^{-1} in winter to ~7.5 μmol m^{-2} s^{-1} in July and August. The total annual soil CO_2 efflux was 841 g C m^{-2} in the dark chamber and 670 and 1089 g C m^{-2} in the two transparent chambers. The soil CO_2 effluxes also closely followed the seasonal and diurnal variations in soil temperature. Soil volumetric water content always remained above 0.2 m^3 m^{-3} during the study period (Fig. 3), which is well above the threshold values that limit microbial activity or photosynthesis of the vegetation (Skopp *et al*. 1990, Davidson *et al*. 1998, Pumpanen *et al*. 2003a). The wilting point in the soil at the SMEAR II measurement station was at 0.1 m^3 m^{-3} volumetric water content (Mecke *et al*. 2002). Each of the three automated chambers had a distinct chamber-specific temperature response, the darkened chamber gave an intermediate temperature response (Fig. 2). The seasonal patterns in CO_2 effluxes that were estimated from the temperature response of the dark chamber and measured in 14 manual chambers in the same forest stand at 2–4 week intervals agreed with each other closely. The Pearson correlation coefficient of the relation between the means for manual chambers and the dark automated chamber was 0.91 ($p = 0.001$, $n = 9$). However, the mean flux of the 14 manual chambers was systematically higher than that of the automated chamber. The linear regression equation fitted between the automatic and manual chambers was of the form:

$$F_{manu} = 1.3942F_{auto} - 0.0422, \quad (6)$$

where F_{manu} is the mean CO_2 efflux measured with manual chambers and F_{auto} is the CO_2 efflux measured by the dark automated chamber. The r^2 of the equation was 0.85.

Temperature response of soil CO_2 efflux

The apparent temperature response (Q_{10}) calculated for 7-day periods and averaged over the period from May to November in the darkened chamber was 2.33 ± 0.21 (SE). The corresponding Q_{10} value for the long term fitting was 3.59

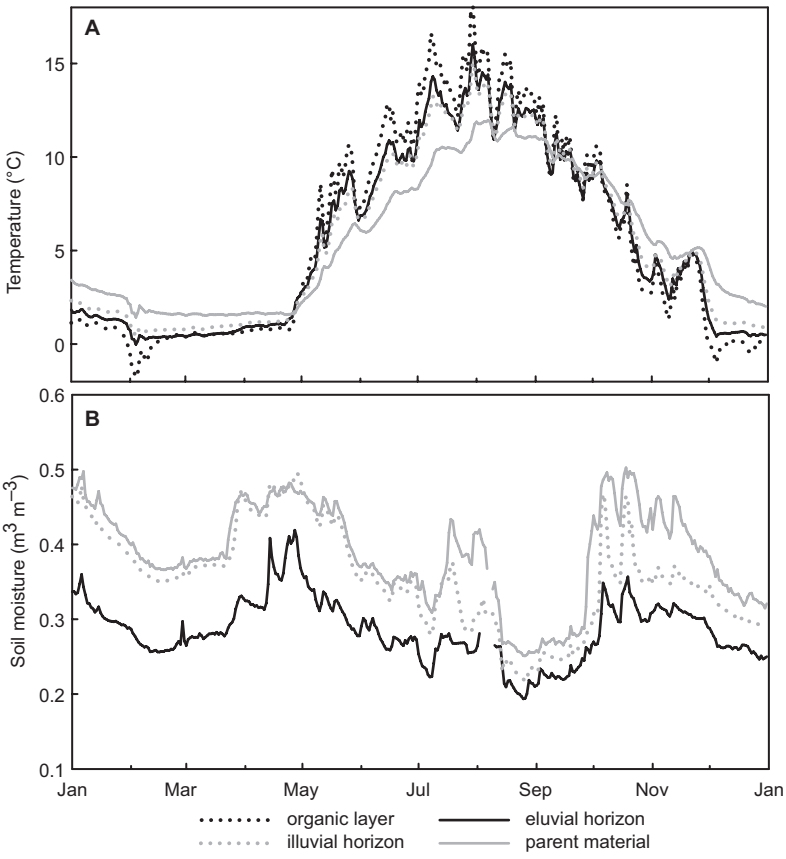

Fig. 3. Seasonal pattern of (**A**) soil temperature and (**B**) soil moisture in the soil layers during the study year 2012.

± 0.03 (SE). The long-term fitting represents the apparent temperature response of the soil CO_2 efflux, which includes the seasonal variation in below-ground carbon allocation of recent photosynthates. The short term Q_{10h} values (mean ± SE = 2.66 ± 0.28 and 2.72 ± 0.25) in the two transparent chambers were not significantly different from each other (p = 0.984) or from that of the dark chamber (p = 0.607 and p = 0.485) when tested with one-way ANOVA (df1,2 = 2,54). The long term Q_{10} (mean ± SE = 3.89 ± 0.10 and 4.75 ± 0.10) values in the transparent chamber were of the same magnitude as in the dark chamber.

Seasonal variation in soil respiration components and GPP

The total soil CO_2 efflux (F_0) in the dark chamber at the annual scale was 841 g C m^{-2} of which 280 g C m^{-2} originated from root and rhizosphere respiration. F_0 and R_h remained constant throughout the winter then started to deviate from each other in late April when soil temperatures started to rise (Fig. 4). The F_0 and R_h values in the dark chamber increased until late July when they reached their respective peaks of 8.65 and 3.81 μmol m^{-2} s^{-1} on 29 July. Similar seasonal patterns were also observed in the transparent chambers. The mean R_a of all the three automated chambers was lowest (17%) in the beginning of April, and reached the highest value of 60% of the total soil respiration on 29 July and started to decline again towards the autumn (Fig. 5).The annual output of R_a contributed about 42% ± 8.9% (SE) to the total soil respiration in the three automated chambers. However, the variation between the chambers was quite large and ranged from 33% to 60%.

The annual total GPP was 1154, and the annual total NEE was 280 g C m^{-2}. There was already some minor photosynthetic uptake in the tree canopy in late winter, but the GPP really started to increase in early April (6 April;

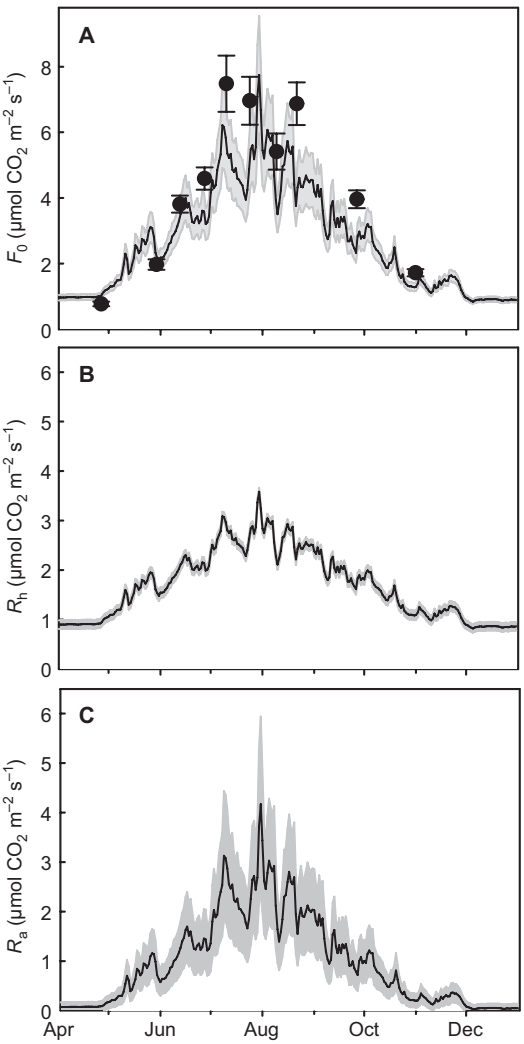

Fig. 4. (**A**) Seasonal cycle of the daily mean soil CO_2 effluxes (F_0) measured by the darkened automated chamber covered with aluminum foil (black line) and the manual chambers (dots). (**B**) Seasonal cycle of the daily means of the estimated component fluxes R_h, and (**C**) R_a in 2012. Error bars represent the standard error of the manual measurements and the gray area the standard error of three automatic chambers.

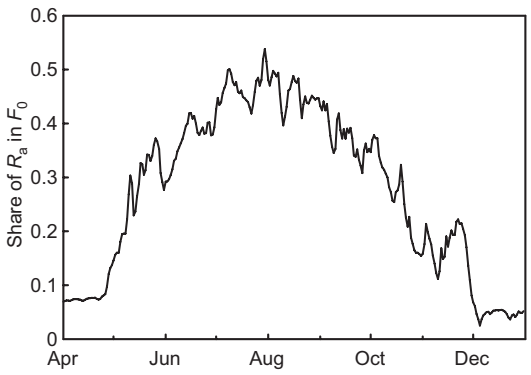

Fig. 5. Seasonal cycle of the daily mean of the contribution of R_a to F_0 estimated using the measurements in the darkened automatic chamber.

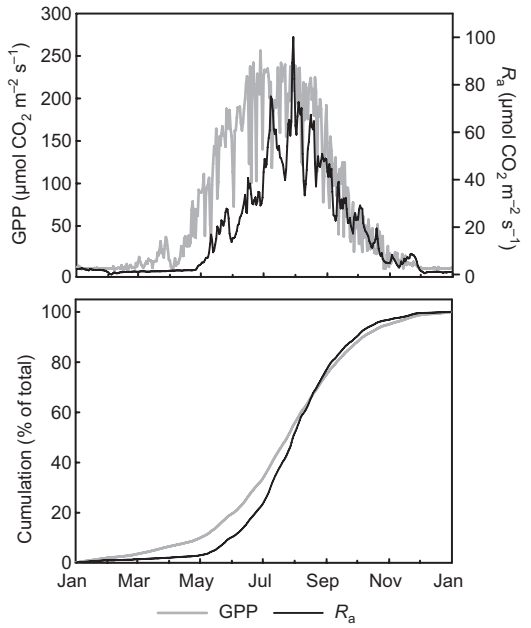

Fig. 6. (**A**) Daily GPP and R_a, and (**B**) their accumulation in 2012.

Fig. 6). The rapid increase in the GPP lasted until mid-summer. The GPP remained at the same level until mid-August when it started to decline until the end of November. A similar pattern was observed for the NEE. The random and systematic uncertainty related to the annual GPP derived from the eddy covariance measurements is approximately 20 and 100 g C m^{-2}, respectively (Kolari *et al*. 2009).

There was a clear time lag between the increase in photosynthesis in April and R_a output. The R_a started to increase on 24 April, 18 days after the onset of GPP (Fig. 6). The increase in R_a was connected to the thawing of the soil and consequent rapid increase in soil temperature. In April, R_h started to deviate from R_a. The deviation was related to the inherent assumption of the calculation procedure because both R_h and R_a were calculated using the temperature response. There was an even larger time lag between the

dates when the highest GPP and R_a were reached (25 June and 29 July, respectively) (Fig. 6). GPP remained at a high level for about 6 weeks until it started to decline on 5 August.

Discussion

Contribution of autotrophic and heterotrophic soil respiration

The soil CO_2 efflux values measured in this study are well within the range of those reported in earlier studies conducted in boreal coniferous forests (Morén and Lindroth 2000, Rayment and Jarvis 2000, Domisch *et al*. 2006, Niinistö *et al*. 2011). The contribution of R_a reached its highest value in late July, which coincided with the maximal fine-root biomass and living fungal biomass. The living fine-root biomass has a seasonal variation whereby the largest biomass occurs in late summer and autumn (Hanson *et al*. 2013). The root and rhizosphere respiration thus followed the carbon allocation pattern of trees, which in turn followed a seasonal variation that followed the phenology and ontogenetic development of trees. During the shoot extension and needle unfolding phases, more carbon was probably allocated to above-ground than to below-ground parts. Maximum root growth occurs when shoot growth has come to an end (Konôpka *et al*. 2005).

The annual contribution of R_h and R_a in our study agrees quite well with earlier studies that used a physiological manipulation or isotope labeling technique which found that as much as half of the carbon released in soil respiration was derived from recent photosynthate (Högberg and Read 2006). However, the estimates are highly variable and mostly range between 30% and 70% of the total soil respiration (Nakane *et al*. 1983, 1996, Ewel *et al*. 1987, Bowden *et al*. 1993, Hanson *et al*. 2000, Maier and Kress 2000, Epron *et al*. 2012). The novelty of the method used in our study lies in the determination of R_h and R_a on a continuous basis for small time intervals. Earlier field experiments were usually based on girdling, trenching or pulse labeling, which are inherently destructive or do not allow for determination monitoring of respiration.

Our method for R_a estimation is rather sensitive to the parameter r_0 and to temperature response values used in the calculation. The long-term temperature responses, or apparent temperature responses in soil respiration measured in this study were relatively strong but were still within the range of those measured earlier in boreal-forest studies. The temperature response Q_{10} values measured in the boreal forest soils range form 0.98 (Gulledge and Schimel 2000) to 4.75 (Morén and Lindroth 2000), but typically the values presented in the literature vary between 2 and 3. The Q_{10} values in our study were close to those measured by Pumpanen *et al*. (2003b) at the same forest site using a static chamber method. This Q_{10} value is probably a conservative estimation because the static chamber technique has a tendency to underestimate soil CO_2 effluxes (Pumpanen *et al*. 2004).

When comparing the temperature response of soil CO_2 efflux chamber measurements in the field, one has to take into account the measurement depth, which has a substantial effect on the temperature response. The temperature response reflects the diurnal amplitude in the soil temperature, that has a large vertical stratification. The deeper the soil temperature is measured, the smaller is the temperature variation and the higher obtained Q_{10} (Pavelka *et al*. 2007, Graf *et al*. 2008). Ideally, the temperature measurement depth should be based on the biologically most active soil layer. Therefore, in our study, the temperature was calculated as a mean of the humus and the mineral soil layer closest to the soil surface where the root density is highest at this measurement site (Ilvesniemi and Liu 2001).

The short-term temperature responses of Q_{10h} were similar to those measured using a laboratory incubation technique. For example, Kähkönen *et al*. (2001) measured Q_{10} of 2.3–2.8 for microbial respiration at the same measurement site as used in our study. This gives us confidence that our short-term temperature response values represent the soil microbial respiration well because in the study by Kähkönen *et al*. (2001) respiration was measured from soil core samples from which the roots were removed before the respiration measurements in the laboratory.

Soil respiration components and GPP

The total annual soil respiration in this study was about 75% of the total GPP of the forest, and the root and rhizosphere respiration was 45% of the annual GPP. The magnitude of these fluxes represent a substantial contribution to the forest carbon balance. Kolari *et al*. (2009) reported that the GPPs of trees and ground vegetation were 914 and 117 g C m^{-2}, respectively, and the soil respiration was about 606 g C m^{-2}. The proportion of soil respiration reported in the study of Kolari *et al*. (2009) was about 59% of the annual GPP. In our study, the proportion was higher (75%) which may be due to methodological differences between the two studies (Pumpanen *et al*. 2004). In the study of Kolari *et al*. (2009), soil CO_2 effluxes were measured using a flow-through chamber described by Pumpanen *et al*. (2001). The measurements made by Kolari *et al*. (2009) were adjusted by spatial sampling conducted with a portable closed dynamic chamber on 12 measurement plots. In our study, we used a novel chamber based on the Vaisala GMP343 CO_2 sensor which was installed inside each chamber's headspace. Nevertheless, the chamber method does not affect the seasonal pattern of the CO_2 efflux and its temperature response fitting. Thus, we are confident that the temporal dynamics in our CO_2 efflux measurements are correct.

There was a substantial time delay between the onset of GPP of the trees and the start of the increase in R_a. Ťupek *et al*. (2008) also observed a considerable delay in soil respiration at another measurement site nearby this study site. This may be related to the differences between the phenological processes that take place above and below ground. Usually in early spring to mid-April, the soil is still cold after the winter and the temperatures are near 0 °C until mid-April and are still below 5 °C until mid-May. The autotrophic respiration value was derived by subtracting heterotrophic respiration from total CO_2 efflux, whereas heterotrophic respiration was calculated based on short-term temperature responses fitted over 7-day periods. Thus the low soil-temperature in early spring is reflected in the autotrophic respiration values obtained using Eq. 5. The temperature of 5 °C is considered a threshold value for the start of the growing season, and in the soil surface layers at the measurement station this temperature was reached more than two weeks later (9 May 2012) than in the air (22 April 2012) (data not shown). This time lag was also reflected in the carbon allocation whereby the recent photosynthates were allocated to the growth of above-ground parts such as new shoots and needles, which in southern Finland occurs from mid-May to mid-June. At the site, the new needles and shoots usually reach their maximum length in mid-June (Schiestl-Aalto *et al*. 2013). The growth of new, fine roots usually reaches its maximum at the latitude of southern Sweden in late July–early August (Hansson *et al*. 2013) and thus coincides with the maximum R_a in late July as observed in our study. The normal temperature-related pattern in soil CO_2 efflux breaks down in early July, which is most likely related to the increased respiration of new root tips. In addition, the living fungal biomass and microbial biomass reach their maxima in late summer, which thus leads to increased soil CO_2 efflux. This deviation in the temperature responses is accounted for in our modeling approach of measuring short- and long-term temperature responses, and it results in an increasing proportion of R_a in the late summer.

Our novel method for determining soil respiration components produced comparable proportions of CO_2 fluxes to those of other methods such as girdling or trenching. However, our method does not interfere with the soil system, and it could be successfully used for continuous, long-time monitoring. We were also able to detect a substantial time lag between the onset of GPP in the spring and the increasing contribution of the autotrophic respiration component in soil CO_2 efflux (R_a). This novel method provides a good tool to model the intra-annual variation in C flux components in boreal ecosystems, and it can also be applied to any ecosystem that has a clear seasonal pattern in the GPP.

Summary

The start of root and rhizosphere respiration showed a very clear seasonal pattern which followed the GPP of the forest. There was a time lag of 18 days between the onset of GPP

and start of root and rhizosphere respiration in the spring (R_a). Root and rhizosphere respiration contributed about 42% of the total soil CO_2 efflux, but their combined contribution was seasonally extremely variable. The contribution of root and rhizosphere respiration was 45% of the annual total GPP of the forest ecosystem. The highest contribution from the root and rhizosphere respiration were observed at the end of July, which is also the period of highest living fine-root biomass in addition to the fungal biomass. Our method enables continuous determination of root and rhizosphere respiration in an undisturbed manner.

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